Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

ON THE SKULL OF NYCTODACTYLUS, AN UPPER CRETACEOUS PTERODACTYL.

ELSEWHERE I have published a brief description, with a restoration,[1] of an unusually complete specimen of *Nyctodactylus*, recently collected by my assistant, Mr. H. T. Martin, in western Kansas. At the time this restoration was made, the skull was lying in its original matrix, with its palatal surface uppermost. On account of its extreme delicacy, it was thought best then not to attempt its removal. This, however, has since been done in a most skillful manner by Mr. Martin, and it is now almost completely removed from the chalk in which it was embedded. Its delicacy and fragility may be suspected from its weight, scarcely thirty grammes, the mandible weighing about nine grammes more. The remarkable perfection and relative freedom from distortion render the specimen especially valuable for study. The mandible was displaced, in no wise obscuring other parts. The skull is of course depressed, but not so much as one might expect from the position in which it was lying, and there is a slight lateral compression to the right, but not enough to render the interpretation of the characters at all difficult. I give herewith a photographic reproduction of the back part of the skull, as it was seen before removal from the matrix. The anterior portion, on a separate block of matrix, has been omitted in order to show the hyoid bones lying partly beneath it. In the drawings I have attempted to restore the skull as nearly as possible to its living condition. There is yet a possibility that I have made the skull a little too broad, but, if so, the exaggeration must be so small as to be scarcely appreciable. The drawings were made by myself, at least insuring a careful study of the parts.

The premaxillary doubtless comprises the whole anterior portion of the beak, as in other known pterodactyls. In the middle behind, it separates the nares by a rather broad, gently convex or laterally flattened bridge of stout bone, gradually and nearly uniformly decreasing in width posteriorly to an acute point between the frontals near the middle of the orbits. Its margins are rounded as far back as the union with the anterior processes of the frontals, which continue the same convex borders to the free margin of the orbits. The sutures separating the bone from the frontal posteriorly are indicated by lines exactly alike on the two sides, and hence evidently sutural. On the sides the union with the maxillæ is indeterminate. If this union is as in *Rhamphorhynchus*, as described by Woodward,[1] its position would be back of the anterior end of the nares. In *Scaphognathus*, however, Plieninger[2] would locate the suture at the anterior extremity of the nares. Its alveolar borders form straight, sharp, smooth ridges, with the inner wall two or three millimeters in width, meeting the palatal surface at an angle of about 135 degrees. The middle portion above is regularly rounded, forming an arc of about a third of a circle. This portion has its walls distinctly thicker than elsewhere, and has resisted compression; the sides from this median convexity seem to have been gently convex, meeting the middle convexity in a shallow groove. The surface is smooth, as in *Ornithostoma* (*Pteranodon*), without pits or depressions. As in that genus the texture of the bone of the beak has a distinct fibrillation longitudinally, sufficiently well marked to enable one to distinguish fragments from this part of the skeleton; a fact long since recognized by collectors of these animal remains in the field. I am convinced there were no pits, depressions, or conspicuous foramina on the premaxillary, and that neither in this genus nor in *Ornithostoma* was there a longitudinal ridge in the middle above. The proof of this is positive in both this genus and in *Ornithostoma*. On the under side, the bone forming the palatal surface, in part probably composed of the premaxilla, in part of the vomers, is of extreme tenuity, of the thickness of ordinary writing paper. It appears to have been gently concave throughout and smooth; on the sides between this bone and the roof the space was more or less filled in with a loose cancellated bone, but under the convexity of the middle there was a considerable cavity. On the under side of the premaxillary, back of the anterior ends of the nasals, are two pits or depressions, separated by a low ridge, evidently rhinencephalic fossæ.

---

[1] *American Journal of Anatomy*, Vol. I, p. 297.

---

[1] *Ann. Mag. Nat. Hist.*, Vol. IX, No. 2, 1902.

[2] *Paleontographica*, Vol. XLI, p. 203, 1894.

The frontal bone is broad, unpaired, smooth, and nearly flat. Anteriorly it extends forward on either side as far as the posterior end of the nares, receiving between its two pointed processes the posterior pointed extremity of the premaxillary, as already described. There is no indication whatever of a median crest, a fact to which doubtless is due the position of the skull upon its dorsal surface, a position which I have never observed in specimens of *Ornithostoma.* Plieninger speaks of a rudimentary frontal crest in *Pterodactylus,* and its entire absence in this genus is remarkable. Posteriorly, the union with the parietal is indeterminable. On the sides it forms the horizontal, thin, superior border of the orbit for a little more than its posterior half, terminating in an angle a little before the beginning of the attachment of the postfrontal. At the anterior angle the border turns inward with a concavity looking forward, and then curves forward to be continuous with the sides of the premaxillary. The parietal, or fronto-parietal, continues the plane of the frontal in a long, U-shaped plane, forming the rounded posterior extremity of the skull. The sides of this slender U form the inner and front margin of the supratemporal fossa; from this slightly convex margin posteriorly the parietal descends downward and outward in a thin wing, articulating at the extremity with the posterior flattened end of the squamosal. This wing-like process narrows anteriorly to be continuous with the sides of the braincase.

The nasal is a slender bar of bone, beginning on the under side of the premaxillary, a little back of the middle of the nares, and extending downward and outward to unite with the ascending process of the maxilla to form the posterior boundary of the nares. Posteriorly it is a cribriform plate filling up the concave sinus in front of the prefronto-lachrymal bone. The bone evidently continues over the outer surface of the maxillary process to unite with the lachrymal, and perhaps also with the ascending process of the malar. On the under side of the premaxillary the bones of the two sides may meet in the middle, though this seems doubtful.

The prefrontal and lachrymal cannot be distinguished from each other, and there seems to be some disagreement among writers as to which of the two elements should be called the prefrontal, were they distinguishable. The prefrontal must be that portion articulating along the sides of the premaxillary and frontal, while the lachrymal is that part which forms the anterior or anterior superior border of the orbit, either articulating directly with the frontal and the prefrontal, or with the prefrontal only, which one should expect. In the present specimen the compound element is sharply distinguishable from the frontal and premaxillary, as also the nasal. It begins on the side of the premaxilla a little back of the visible surface of the nasal, to which it is attached, as a slender pointed anterior process, and widens out posteriorly, forming a concave border, to which the thin, imperfectly ossified posterior part of the nasal attaches. Externally it widens out again into the broader horizontal plate forming the anterior superior roof of the orbit, which anteriorly curves downward to meet the jugal. Its orbital margin is thin.

The jugal bone extends forward on the outer and inferior side of the maxilla to beyond the middle of the nares. How far front it goes cannot be determined. In *Ornithostoma* the distinguishing suture, placed as in *Nyctodactylus*, seems to be continued as far forward as the anterior end of the nares, which would seem to indicate that the premaxilla does not reach as far back as in Rhamphorhynchus. At the front extremity of the orbit it sends up a slender process of bone, superimposed upon a thin expansion of the maxilla, to meet the lachrymal and nasal. Beyond this it forms a narrow bar, four or five millimeters in width, to the lower extremity of the quadrate, and then turns upward and backward a little more broadly to join, by a long squamosal suture, the outer side of the quadrato-jugal, forming the anterior superior boundary of the lower temporal vacuity. In *Ornithostoma* it very clearly unites above with both the quadrato-jugal and postfrontal, and in all probability the same relations obtain in *Nyctodactylus*, but of this I am not sure.

The supratemporal bar is evidently formed of two bones, as in *Ornithostoma.* The superior one, joining the outer angle of the frontal (and parietal), is clearly the postfrontal or postfronto-orbital. It extends backward to the head of the quadrate, also touching the squamosal, and probably also joining the jugal, as in *Ornithostoma.* The inferior outer part of the bar, uniting with the jugal, as described, anteriorly, the head of the quadrate, and apparently also the squamosal posteriorly, is, I suppose, the quadrato-jugal, though it corresponds precisely in position and relations with the bone I have called the prosquamosal in the mosasaurs, following Baur. This bone in these and other lacertilians has, at various times, been called the prosquamosal (Baur, Williston), the quadrato-jugal (Gegenbaur, Merriam, Baur), the squamosal (Owen, Huxley, Cope, Baur), and the supratemporal (Cope). In this pterodactyl the bone does not descend to separate the jugal from the quadrate. This, according to Seeley, is sometimes the condition among the pterodactyls. If so, the element must surely be the quadrato-jugal, and not the prosquamosal.

The squamosal seems clearly defined. It is a triangular, curved bone. A small process runs forward to join the post-frontal and "quadrato-jugal;" a broader and flat one curves downward and inward to join the wing-like squamosal process of the parietal, forming the parieto-squamosal arch, while a third joins the opisthotic (paroccipital), and probably also the head of the quadrate. It thus helps to form a small vacuity on the occipital region, between the opisthotic, parietal, and squamosal — the supraoccipital vacuity. It has nothing to do with the braincase, as Seeley thinks it has in the European forms.[1]

The occipital condyle forms something less than a hemisphere, smoothly rounded, and with a small pit in its center. It seems to have looked downward and backward at an angle of about 45°, though it is possible that its angle with the horizontal plane of the skull may have been slightly greater. The basioccipital forms a rounded, somewhat concave and roughened surface, clearly directed at a considerable angle backward. The paroccipital process is a broad, flattened bar, directed outward, backward, and somewhat upward to join the squamosal and quadrate broadly. Above them there is a small vacuity, as already described, while the outer extremity expands to join closely the inferior posterior surface of the quadrate, reaching nearly as far as their middle. The supraoccipital is directed upward and backward, joining the parietal in forming the posterior flattened prolongation of the skull. Their separation cannot be made out, but the two together form a considerable concavity looking downward and backward, with a slender median crest — the occipital crest — along the outer two-thirds.

---

[1] SEELEY, *Dragons of the Air*, London, 1901.

The quadrate is more narrow above, and is firmly united with the opisthotic, squamosal, and "quadrato-jugal" above ; below and to the outer side with the jugal ; internally below with the pterygoid. The articular surface looks more nearly downward. The transverse axes of the two join each other at an angle of about 20°. Each has a deep oblique trochlear groove running from within outward and backward, with the stronger convexity at the inner extremity. The basi-sphenoid is an elongated, flattened, or slightly convex bone, somewhat wider in front than behind, with concave sides, and situated in the same plane with the pterygoids and palate. It joins the pterygoids at each anterior angle broadly and flatly.

The pterygoid is firmly and indistinguishably united with the quadrate at its lower inner extremity, close to the articular surface, by a broad process which ascends slightly to the plane of the palate. The two bones are separated from each other throughout their entire length, or at most touch each other by the slender tips of the anterior inner processes. Anteriorly the bone divides into two unequal processes — a slender one, directed inwardly and anteriorly, closely approaching or touching its mate in the plane of the palate ; and a larger one, which goes forward to beyond the middle of the narial vacuity, articulating with the ectopterygoid, and distally, by a long suture, with the palatine. Between the two there is an arrow-shaped vacuity posteriorly, bounded behind by the basi-sphenoid, the indentation for the head of the arrow formed by a small, thin inner process. This form of the pterygoid, it will be seen, is quite different from that figured and described by Woodward in Rhamphorhynchus. The slender inner process does not turn upward to meet a vomer, as Woodward thinks may be the case in the skull described by him, and the processes which, in his specimen, turn inward and upward are, in *Nyctodactylus*, closely applied to the inner side of the palatines. The pterygoid does not unite with the vomer in *Nyctodactylus*.

The ectopterygoids are thin, narrow bones, articulating broadly with the outer margin of the pterygoid, and exteriorly with the inner side of the slender posterior extremity of the maxilla. The bone is directed forward and outward, its concave margins forming the anterior and posterior borders of the pterygo-jugal and posterior palatine vacuities.

The palatines are long, narrow, thin bones, articulating by a long suture on the inner side with the pterygoid, and on the outer side with the maxilla. Anteriorly the union with the maxilla or vomers is indeterminable.

The relations of the maxilla can be made out only in its posterior part. Its union with the jugal has already been indicated. Posteriorly it sends up a thin, curved process to meet the nasal, forming the posterior inferior boundary of the nares. Back of the thickened portion of this process there is a thin plate reaching back under the superior process of the jugal, the bottom of an oval depression or excavation, which clearly corresponds to the antorbital vacuity of the earlier pterodactyls. From this it is evident that the antorbital vacuity is not united with the nares in either this genus or *Ornithostoma*.

The vomer cannot be made out. If it forms a part of the palatal surface, it is so indissolubly united with the maxillæ, palatines, and premaxillary that no signs of its union can be detected. One thing is certain, it does not separate the narial vacuities, and in all probability it does not touch the pterygoid at all.

Mandibles.—The mandibles are preserved nearly complete, their tip only being wanting—the portion which led to the detection of the specimen as it protruded from the chalk. It was lying horizontally, with the under surface uppermost, but has been entirely removed from the matrix. It has suffered a slight lateral compression to the left.

The cotylar cavity fits well on the condyles of the quadrate. The projection back of the articulation is very slight, less so than in *Ornithostoma.* The rami are slender, flattened from within outward, and are broadest at about their middle, the upper thin margin being gently convex from near the cotylus to as far forward as the symphysis, which begins about fifty millimeters in advance of the anterior end of the external nares. From the beginning of this symphysis, diminishing in width to the anterior extremity, the under margin is convex, not carinated. About twenty-five millimeters back of the true symphysis of the dentaries there is a symphysis of the thin bone which forms the floor of the mouth. This forms a thin, deeply curved hind border joining rami about midway between their upper and lower margins. The floor of the mouth from here onward seems to have been, like the opposing palatine surface, smooth, and nearly plane. The space between these surfaces, was, however, somewhat greater posteriorly than anteriorly, since the alveolar parapet is considerably deeper posteriorly. The concave posterior margin of the floor is about twenty millimeters in front of the anterior end of the internal narial vacuity. Anteriorly the margins of the mandibles are as in the upper jaws. In cross-section through the symphysis the mandible was, I think, somewhat concave or partly plane on the sides, with the under margin convex, not convex throughout, as I have thought might be the case in *Ornithostoma.* The mandible certainly could not have possessed very great strength in seizing.

Openings.—The external nares are large and ovate, looking outward and upward and forward. They are bounded above by the premaxillary anteriorly, the nasal posteriorly, below by the maxilla (and premaxillary anteriorly?), behind by the nasal above and the maxilla below.

The orbits are longer than wide, looking outward and but slightly upward and forward. The superior emargination above (doubtless roofed over in life by the integument) if not taken into account would leave the orbit oval in shape, with the anterior end rather broader than the posterior. It was bounded above by the frontal, prefrontal, and lachrymal, by the lachrymal and malar in front, the malar below and behind, and the postfrontal in part behind. It had a ring of thin, large sclerotic plates, which were preserved in displaced positions. The separate plates were not united by imbrication, as in the mosasaurs.

The supratemporal vacuity is broadly oval in shape, deep anteriorly and shallow posteriorly, bounded on the inner side by the parietal, on the outer side by the postfrontal and squamosal, and behind by the margin of the squamosal and parietal process. It opens anteriorly into the spheno-quadrate vacuity, and has a narrow slit between the squamosal and opisthotic. The infratemporal vacuity is long and narrow, broader posteriorly. It is bounded on the inner side and behind by the quadrate, externally and above by the jugal and the quadrato-jugal. The large oval vacuity between the quadrate and the basi-sphenoid is broadest at the middle, bounded in front by the quadrate process of the pterygoid, behind by the paroccepital process. The pterygo-jugal vacuity is irregular and elongated, bounded behind by the articular end of the quadrate, on the outer side by the jugal and maxilla, on the inner side by the pterygoid posteriorly and the ectopterygoid anteriorly. The posterior palatine vacuity is a small oval vacuity placed obliquely between the ectopterygoid behind, and the palatine in front, barely touching, if at all, at the extremities the pterygoid and the maxilla. The interpterygoid vacuity is arrow-shaped, placed between the basi-sphenoid posteriorly and the pterygoids on the sides. The narial vacuity is a very large opening, oval in general shape, but with a triangular projection behind made by the two inner processes of the pterygoids, and a smaller triangular process in front extending back from the roof of the mouth. It was not divided in the middle and was doubtless covered over for the most part by membrane pierced by the internal nares.

The skull of *Nyctodactylus*, while presenting very great resemblances to that of *Ornithostoma* (*Pteranodon*) differs in important characters. Its quadrate is much shorter, terminating below in the condyle for the mandible nearly below the middle of the orbit, while in *Ornithostoma* the articulation is in advance of the orbit. The orbit and supratemporal vacuities are proportionally larger, and there is no crest, not even a rudimentary one. The bar between the orbit and the nares is narrower, the frontal bone less broad relatively in *Ornithostoma*.

In *Nyctodactylus* we have a less highly specialized type of pterodactyl than is seen in *Ornithostoma* as is evidenced by the absence of the crest, the plane frontal bone, and the less oblique position of the quadrate. On the other hand the genus has the same type of skull, and toothless jaws, and the general proportions of the skeleton throughout are the same. I believe that the resemblances between the two genera are of much greater importance than the differenees. These differences rest in the non-articulation of the scapula with the supraneural plate of the vertebræ, in the absence of crest, and the position of the quadrate especially. Both forms are toothless. If much importance is given to the scapular articulation the two genera must go into different families at least — *Ornithostoma* among the Ornithocheiridæ, and *Nyctodactylus* with the Pterodactylidæ. But such a severance is, I, believe, questionable. It is a rather curious instance of parallel growth that has brought about the toothless forms of *Ornithostoma* from the toothed *Ornithocheirus*, and the toothless *Nyctodactylus* from the toothed *Pterodactylus*; possibly this has been the phylogeny. On the other hand, it would also seem possible that the same toothless form has been ancestral to both

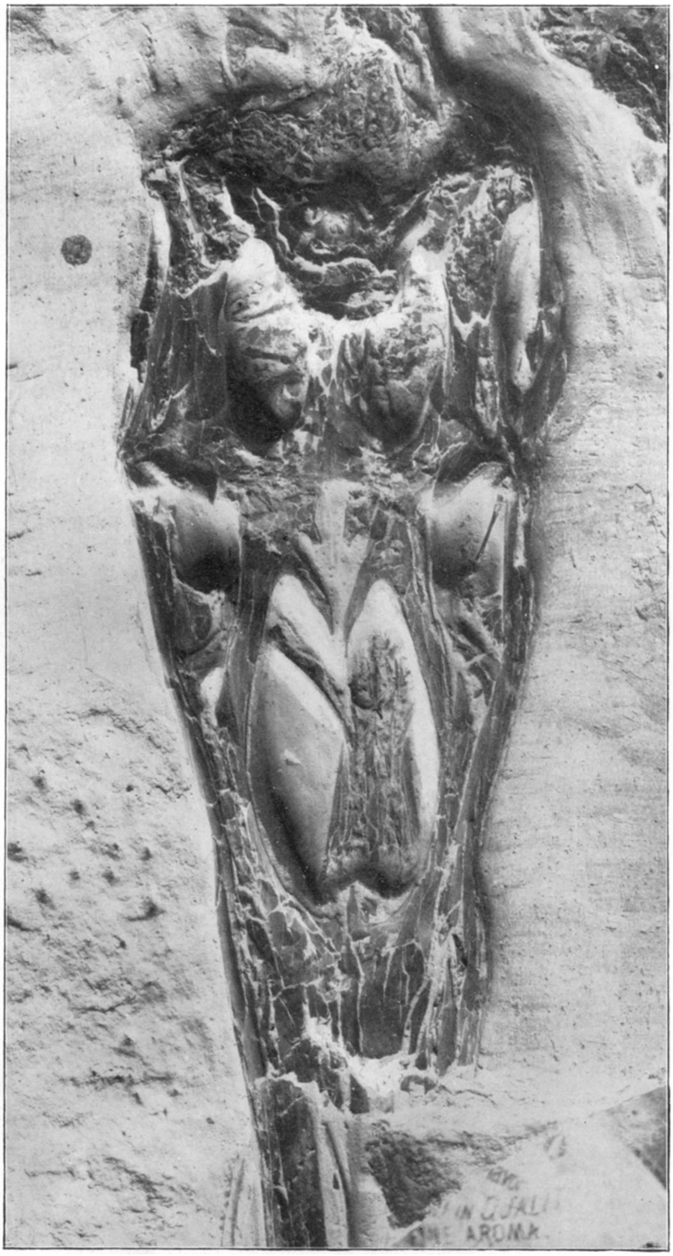
Nyctodactylus, the lesser, and *Ornithostoma*, the more, specialized type.

If my interpretation of the elements of the skull of *Nyctodactylus* is correct, I fail to see any marked avian resemblances in it. The only character that might be considered as such is the undivided narial vacuity, aside from the lightness of the bones and their closely united sutures, both adaptive characters. The supratemporal arch is purely reptilian, as is the presence of the ectopterygoid, etc. The union of the premaxillary with the frontal is found in the plesiosaurs. A further discussion of this question I hope to present in a future paper, in which I shall give a more detailed description of the remainder of the skeleton, with illustrations.

I am convinced that the arrangement of the ribs back of the sternum, not only in *Nyctodactylus*, but in other pterodactyls, is different from what has been generally supposed and figured. They extended outward in the plane of the wing membrane, which they served in a measure to support, and did not enclose the ventral cavity. From a recent examination of the type of *Rhamphorrhynchus phyllurus* Marsh, I am satisfied that this was their function in that animal, and I doubt not it was also in all other pterodactyls. This difference in function accounts satisfactorily for the marked contrast in slenderness between the anterior and posterior ribs, as also for the slight curvature of the latter.

The hyoid bones of the present specimen are quite like those of other pterodactyls — long, slender rods. They are shown in part in Plate I. At the back of the skull in the same plate is also seen a small triangular or V-shaped bone, which I take to be the proatlas.

It will be of interest to note that in the matrix underlying the skull occurred several specimens of the Cirriped *Stramentum*, together with a vivid impression of a Lepas-like barnacle having a slender, flexible, naked peduncle about 40$^{\mathrm{mm}}$ in length. The capitulum seems to have been enclosed either in chitinous or membranous plates, evidences of which are present, and impres-



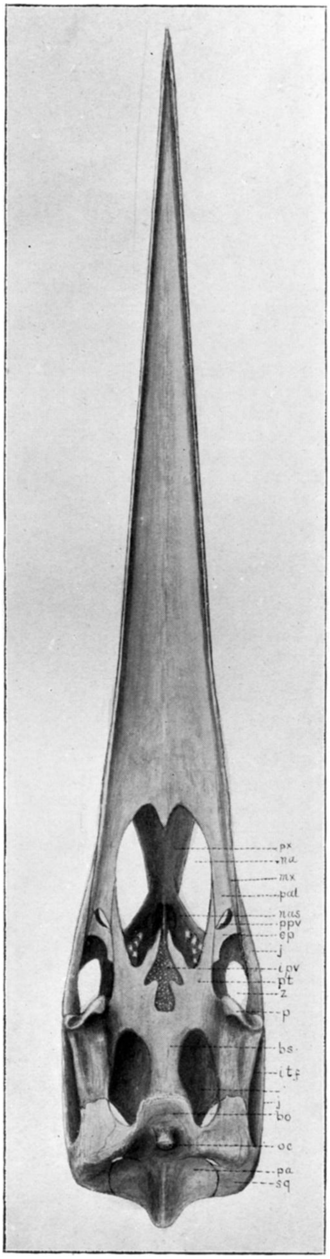

px
na
mx
pal
nas
ppv
ep
j
ipv
pt
z
p
bs
itf
j
bo
oc
pa
sq

FIG. 1.

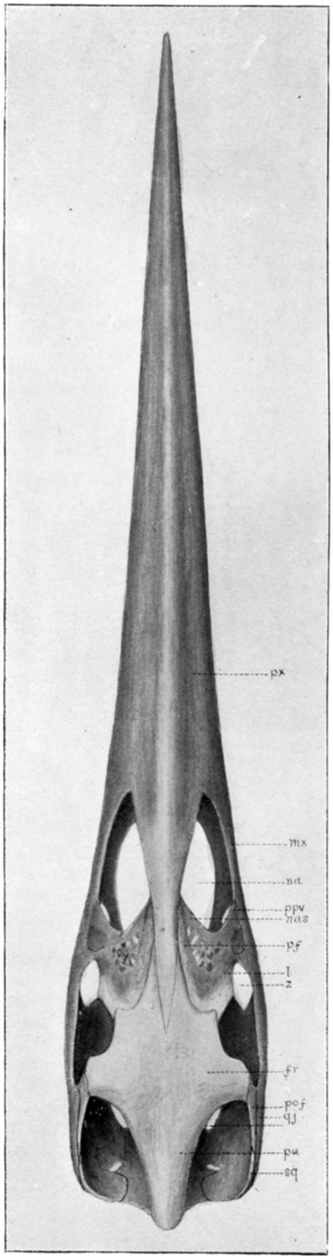

px
mx
na
ppv
nas
pf
l
z
fr
pof
qj
pa
sq

FIG. 2.

sions of the cirri are plainly present. Other impressions of phyllopods or ostracods are also abundant in the matrix.

S. W. Williston.

University of Kansas,
Lawrence, April, 1902.

EXPLANATION OF PLATES.

Plate I. Under surface of posterior part of skull, lying in the matrix slightly enlarged. Near the anterior end are seen the two hyoid bones, and in the occipital region, the small, triangular proatlas.

Plate II. Fig. 1, Under view of skull; Fig. 2, upper view of same, both a little more than half natural size; *bo*, basi-occipital; *ep*, ectopterygoid; *fr*, frontal; *ipv*, interpterygoid vacuity; *itv*, infratemporal vacuity; *j*, jugal; *l*, lachrymal; *mx*, maxilla; *na*, nares; *nas*, nasal; *oc*, occipital condyle; *pa*, parietal; *pal*, palatine; *pf*, prefrontal; *pof*, postfrontal; *ppv*, posterior palatine vacuity; *px*, premaxillary; *q*, quadrate; *qj*, quadrato-jugal; *sq*, squamosal; *z*, pterygo-jugal vacuity.